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Habitat Use and Ranging of Wild Bonobos *(Pan paniscus)* at Wamba

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The relationship between vegetation and ranging patterns of wild bonobos at Wamba, Democratic Republic of the Congo, was examined. Via Landsat data, we distinguished three types of vegetation—dry forest, swamp forest, and disturbed forest—at Wamba. The home ranges of the study groups changed considerably from year to year, due mainly to intergroup relationships. The population density of each group varied between 1.4 and 2.5 individuals per km^2 and was lowest during a period of population increase. Home ranges consisted mainly of dry forest. The bonobos used dry forest more frequently than the other forest types, though they also used swamp and disturbed forest almost every day. The latter types of forest seemed to be important resources for the bonobos, owing to the abundant herbaceous plants that are rich in protein and constantly available. The bonobos tended to use dry forest more frequently in the rainy season than in the relatively dry season, probably because the favored fruits in the dry forest were mostly available in the rainy season. There was no seasonal difference in the size of the daily ranging area.

KEY WORDS: bonobo; *Pan paniscus*; home range; habitat use; Landsat; seasonality.

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INTRODUCTION

While chimpanzees occupy a range of habitats from rain forest to savanna–woodland, bonobos live only in tropical rain forest. However, their tropical rain-forest habitat is not homogeneous, but consists of different types of vegetation, including primary forest, swamp forest, and secondary forest around villages (Kano, 1992; Idani *et al.*, 1994). Idani *et al.* (1994) reported that all of these types of forest have many kinds of food trees for bonobos.

Some reports about habitat use of bonobos emphasize the importance of primary forest. Bonobos use primary forest almost every day (Kano and Mulavwa, 1984), and its utilization rises during the seasons of favored fruits (Kano, 1992). Bonobos also tend to use primary forest for sleeping sites (Kano, 1992; Idani *et al.*, 1994).

Conversely, some reports stress the importance of swamp forest and secondary forest for bonobos, which often forage there as well as the primary forest (Kano, 1992). They include abundant herbaceous foods that contain more protein than is in fruits (Wrangham, 1986; Kano, 1992; Malenky and Stiles, 1991; Malenky *et al.*, 1994; Idani *et al.* 1994). Bonobos use them frequently during the transition period between fruiting seasons (Kano, 1992).

To obtain a more general view of habitat use by bonobos, we need a quantitative analysis of the relative importance of vegetation types on the basis of long-term data. We analyzed data for two wild groups at Wamba from several observation periods between 1983 and 1996. We determined the vegetation types in the home range via Landsat data and analyzed daily ranging routes to assess the frequency of use of each vegetation type. We also examined changes in the home ranges of these two groups in relation to intergroup relationships.

MATERIALS AND METHODS

We focus on habitat use by two wild bonobo groups, E1 and E2, at Wamba, Region de l'Equateur, Democratic Republic of the Congo (0°02′N, 22°35′E). The temperature of this area is fairly stable throughout the year and the average highest and lowest monthly air temperatures are 30 and 20°C, respectively. Annual rainfall is about 2000 mm. Although it rains throughout the year, there are two rainy seasons and two relatively dry seasons. The light rainy season is from March to May, and the severe rainy season is from September to November. The dry seasons are from June

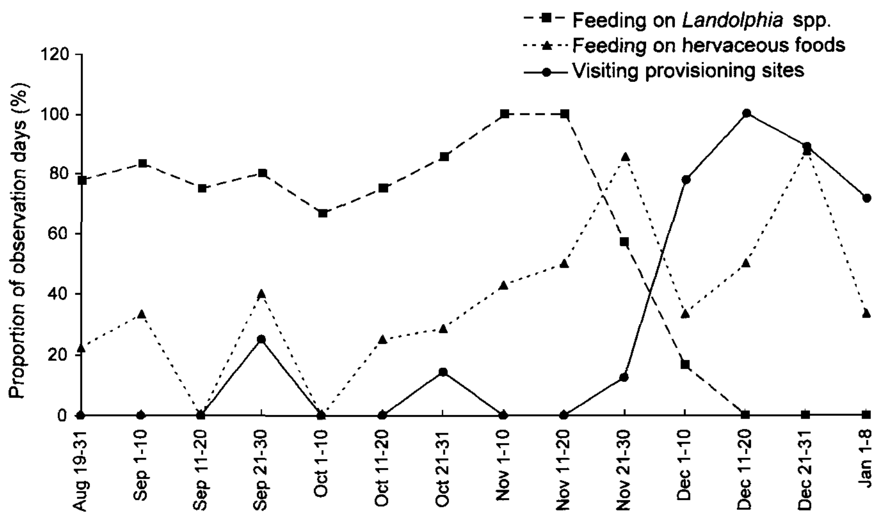

Fig. 1. Seasonal change in use of *Landolphia* spp., terrestrial herbaceous foods, and artificial provisioning sites. While following E1 in 1985–1996, we recorded the main food for each feeding session. This figure shows the proportion of days on which each food was used as the main food in at least one feeding session or the proportion of days on which bonobos visited provisioning sites at least once, to the total number of observation days.

to August and December to February (Kano and Mulavwa, 1984; Kano, 1992).

Studies began of a unit group called E in 1974. E split into E1 and E2 between 1982 and 1983 (Kuroda, 1979; Kitamura, 1983; Furuichi, 1987; Kano, 1992). We conducted our study after the split, in the following 5 periods: August 1983 to February 1984 (E1), August 1985 to January 1986 (E1 and E2), September 1987 to January 1988 (E1), September 1990 to February 1991 (E1 and E2), and April to June 1996 (E2).

The study groups had been provisioned with sugarcane since 1976 (Kuroda, 1979; Ihobe, 1992). They usually appeared at provisioning sites during the dry season. The extent of dependence on the provisioning sites seemed closely connected to the fruiting of the bonobos' favorite foods, *Landolphia* spp. (Fig. 1). The frequency of appearance at the provisioning sites varied greatly from year to year, and this was probably due largely to interannual variation in the fruiting of these species.

We used data from all days in all observation periods to compare home ranges for different groups and periods. To avoid biases due to artificial provisioning, data from periods during which study groups appeared at the provisioning sites on >10% of the observation days are excluded from the analyses of daily ranging area and proportion of vegetation types used. Data

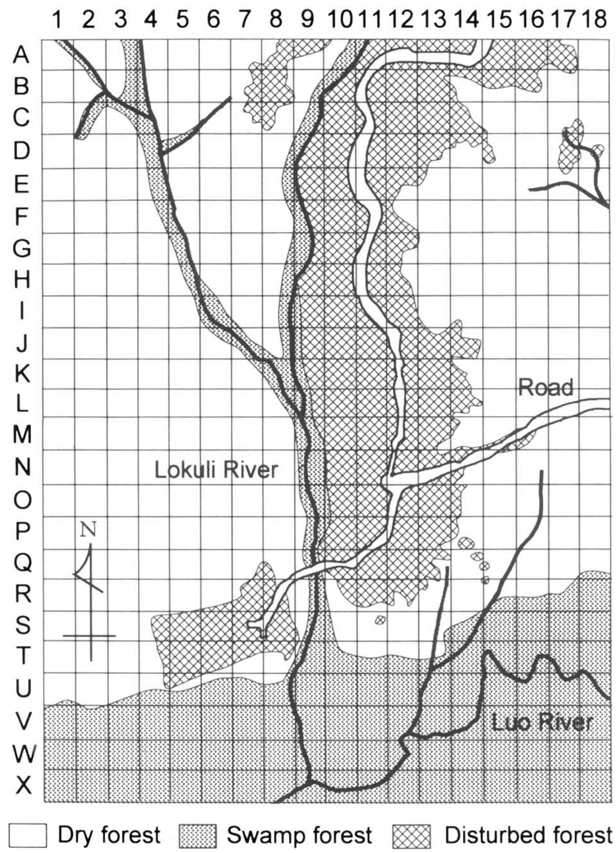

Fig. 2. Vegetation map of the study area. Distributions of dry, swamp, and disturbed forest are based on the composite picture from Landsat data. One grid square represents 500 × 500 m.

from days when either the morning or evening nest site was not confirmed are also excluded from the analyses.

E1 visited provisioning sites only a few times in 1983–1984. Therefore, we used the data from this period for the analyses of daily ranging area and vegetation type usage. In 1985–1986, E1 frequently visited the provisioning sites after December 5, so we used only data recorded before December 5 in the analyses. We used no datum for E1 in 1987–1988 and 1990–1991 because they bonobos intermittently visited the provisioning sites throughout the study periods.

We rarely gave E2 sugarcane at the provisioning sites. We sometimes gave a small amount of sugarcane in the early morning at the sleeping sites to confirm the membership of parties, but this did not seem to influence their ranging pattern. Thus we used the data for E2 from all study periods for all kinds of analysis.

We used Landsat data to make a vegetation map of the study area. They are from the Landsat Scene of Thematic Mapper (TM) sensor [path 178–row 60, 175 km (North–South) × 185 km (East–West)], recorded on January 14, 1991. These data were analyzed by the program ERDAS, Version 7.5. A picture was synthesized by TM bands 5 (midinfrared: 1.55–1.74 mm), 4 (reflective-infrared: 0.76–0.09 mm), and 3 (red: 0.63–0.69 mm) and are represented by red, green, and blue, respectively.

We divided an area covering the home range of E1 and E2 into a grid with squares 500 × 500 m (Fig. 2). We assigned each square to one of the vegetation types if more than two-thirds of it was covered by that type. When two types of vegetation each covered more than one-third of the square, we scored it as evenly divided between the two vegetation types.

Although, like chimpanzees, bonobos have fission and fusion of parties, they usually range as one or two large mixed parties (Furuichi, 1987; White, 1988; Kano, 1992; Elsacker, *et al.*, 1995). We usually followed the largest mixed party and recorded the squares that they visited on each observation day. The daily ranging area is represented by the number of squares that were visited by the party. We counted a square ≥2 times when the party visited it repeatedly on the same day. For the analysis of the daily ranging area, we used data from days on which both sleeping sites in the morning and evening were confirmed.

The daily use of each vegetation type is represented by the frequency of squares visited. Because bonobos rarely moved more than 500 m without a break for other activities, we could assume that the squares visited were actually used by bonobos. When a study group visited a square that was represented by a certain vegetation type, we gave one point to that type. If a study group passed a grid that was represented by two vegetation types, we gave 0.5 point to each type. Then we calculated the proportion of total points of each vegetation type to the total points for all vegetation types for each day. This analysis also used data from the days on which both morning and evening sleeping sites were confirmed.

One might prefer analyses based on the actual time spent in the squares rather than analyses based on the frequency of visits to the squares. However the number of data sets for which data of actual time are available is too small to compare the tendency of habitat use between different groups and different years. Furthermore, analyses based on the actual time might underestimate the use of swamp and disturbed forests because it was very difficult to track and to observe bonobos directly in such vegetation.

We avoided such bias by an analyses based on the frequency of visit to the squares, since we could record the ranging route of bonobos throughout a day by tracing their footprints and vocalizations.

To examine the points, we compared results from the frequency-based analysis an those from the time-based analysis of one data set. The frequency-based analysis showed that in 1983–1984, E1 used dry, swamp, and disturbed forests for 64.2, 20.3, and 15.5%, respectively (Fig. 4b), while the time-based analysis showed that the use of these vegetation types were 68.2, 17.1, and 14.7%. The proportion of use of swamp and disturbed forests is slightly smaller in the time-based analysis because of the less direct observation in these forests, but the differences are not statistically significant. Therefore, we assume that the frequency-based analysis is a reasonable method to evaluate the use of each vegetation type.

RESULTS

Vegetation Types

We can distinguish 3 types of vegetation in the picture produced by Landsat data. Our knowledge of actual vegetation in many parts of the study area indicates that they represent dry forest, swamp forest, and disturbed forest (Fig. 2).

The majority of dry forest in our analysis coincides with primary forest in the vegetation map produced by Kano and Mulavwa (1984), but it also includes areas of old secondary forest on their map. Dry forest is dominated by trees of the Caesalpiniaceae, and some areas have a thick undergrowth of Marantaceae (herbs).

Swamp forest in our study coincides with the findings of Kano and Mulavwa (1984). It occurs along large rivers like the Luo, as well as smaller streams like the Lokuli River. It is mostly primary forest, covered by tall trees, such as *Uapaca heudelotti.* There are many terrestrial herbs including *Aframomum* spp. and *Sclerosperma mannii* in the swamp forests.

Disturbed forest in our study includes young secondary forest and cultivated or fallow land in the study by Kano and Mulavwa (1984). Young secondary forest was usually <10 years old, and it had been used repeatedly for fields. There are many trees of *Musanga cecropioides*, and a thick undergrowth of *Aframomum* spp., *Haumania liebrechtsiana*, and other herbaceous species in disturbed forests.

Table I. Home Range Area, Group Size, and Population Density of Groups E1 and E2

Study group	Study period	Number of squares visited[a]	Home range area (km^2)	Group size (individuals)	Population density (individuals/ km^2)
E1	1983–1984	56	14.0	25	1.8
	1985–1986	71	17.8	28	1.6
	1986–1987	49	12.3	31	2.5
	1990–1991	50	12.5	30	2.4
E2	1985–1986	126	31.5	Ca. 45	1.4
	1990–1991	100	25.0	52	2.1
	1996	90	22.5	35	1.6

[a]Each square was counted once irrespective of the frequency of visits.

Ranging Area

Figure 3 shows the ranges of E1 and E2 in each observation period. The total range used by the bonobos increased to the south and to the west between 1982 and 1983 when E group split (Kano, 1992). Even after the split, the home range of E1 continued to increase until 1986 (Fig. 3a, Table I). During this period, the population density of E1 was lower than during other periods, and the group size of E1 was increasing (Furuichi *et al.*, 1998). In 1986–1987, the home range of E1 decreased, and its population density rose. Then both range area and group size remained at the same level until 1990–1991.

E2 also expanded their home range after the split (Fig. 3b, Table I). The home range of E2 was largest in 1985–1986, when 21.6% overlapped with the home range of E1. In 1990–1991 and 1996, E2 did not use the southern area so much, and the portion of their home range that overlapped with E1 decreased to 4.2%. Although E2 frequently used the northernmost area in 1990–1991, they did not use it as much in 1996, perhaps because they were avoiding hunters in the northern area.

Table II shows the size of daily ranging area. Although the average differed from month to month, there is no consistent tendency between groups or between periods. When data were pooled for each season, there is no significant difference between the rainy and the dry seasons, in any combination of data for different groups or periods. Conversely, there is a significant difference between groups. If all the data are pooled across periods for each group, E1 used a mean of 5.6 squares per day, while E2 used 6.8 squares per day (Mann–Whitney U test, $n1 = 148$, $n2 = 129$, $U = 7238.5$, $p < 0.001$). E2 may have used a wider area each day because its group size was greater than that of E1.

(a)

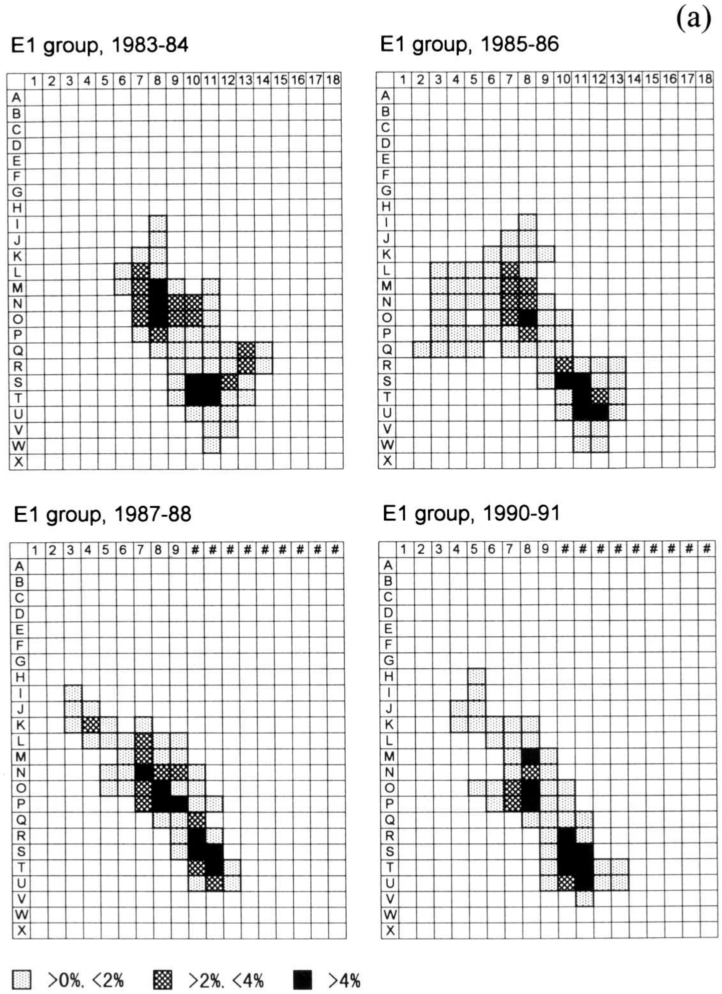

Fig. 3. Home range and relative frequency of use of each grid square for E1 (a) and for E2 (b). The relative frequency is indicated by the proportion of frequency of use of each grid square to the total frequency of use of all squares. Provisioning sites are at O-8 and S-11.

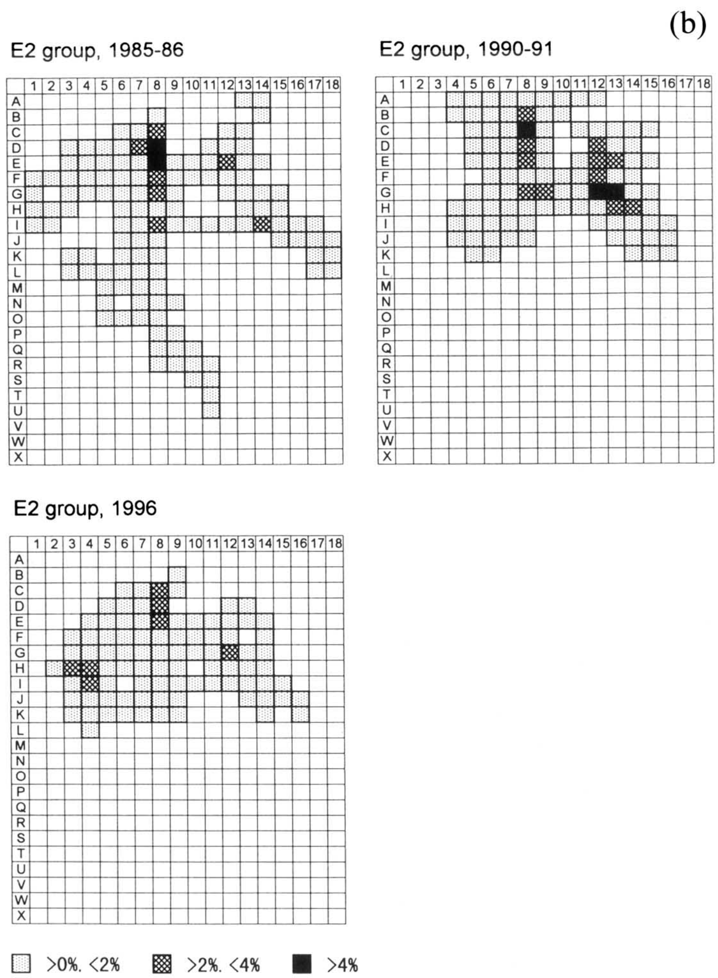

Fig. 3. Continued.

Table II. Average Number of Squares Visited in 1 Day in Each Month and Season

Study group	Observation period	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Rainy season (Sept–Nov)	Dry season (Dec–Feb)	Difference between rainy and dry seasons: Mann–Whitney *U*	Difference between rainy and dry seasons: Probability
E1	1983–1984					3.0[a]	4.6	4.5	5.3	6.2	4.9	5.7		4.7	5.6	1052	n.s.
						1[b]	*12*	*23*	*15*	*22*	*21*	*7*		*50*	50		
	1985–1986					6.0	6.6	7.1	6.4	6.3				6.6	6.3	58	n.s.
						4	*13*	*7*	*20*	*3*				*40*	*3*		
E2	1985–1986					8.7	9.6	6.5	7.0	5.6				7.4	5.6	66	n.s.
						3	*5*	*6*	*12*	*8*				*23*	*8*		
	1990–1991							5.9	6.9	5.5	5.8	8.6		6.4	6.3	516	n.s.
	1996	7.0	6.9	8.8				*14*	*13*	*19*	*13*	*8*		*27*	*40*		
		1	*17*	*10*													

[a]One square was counted ≥2 times when the party visited it repeatedly on the same day.
[b]Figures in italics show the number of sample days in each month or season.

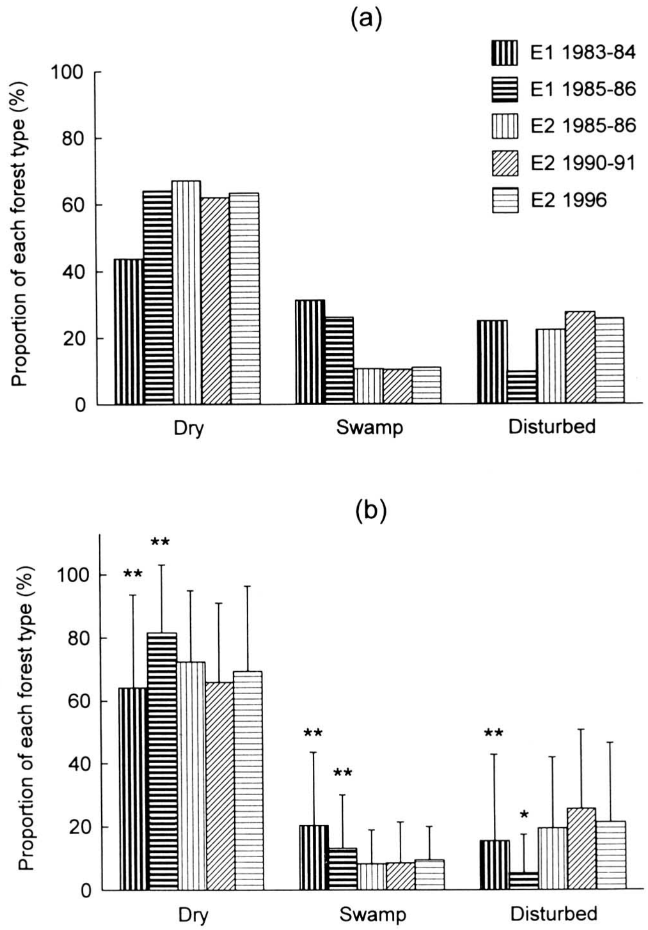

Fig. 4. Percentages of vegetation types in the home range (a), and percentages of vegetation types used (b). In b, bars show the average proportion of each vegetation type used, with lines for the standard deviation.Differences between the frequency of use observed and the frequency expected from the proportion of vegetation types in the home range were examined via the binomial test: $*p < 0.05$; $**p < 0.01$.

Utilization of Vegetation

The proportion of each type of vegetation in the home range of E1 and E2 is shown for each observation period in Fig. 4a. The proportion of dry forest is greater than that of swamp or disturbed forest in the home

Table III. Average Proportion of Vegetation Types Used in Each Month and Season[a]

Vegetation type	Study group	Observation period	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Rainy season (Sept–Nov)	Dry season (Dec–Feb)	Difference between rainy and dry seasons: Mann–Whitney *U*	Difference between rainy and dry seasons: Probability
Dry forest	E1	1983–1984					33.3	58.1	67.6	58.7	55.3	73.3	80.3		62.7	66.4	1076.0	n.s.
		1985–1986					79.0	83.3	77.3	88.2	42.9				84.7	42.9	11.5	<0.05
	E2	1985–1986					76.1	79.0	68.1	78.5	61.0				75.9	61.0	55.0	n.s.
		1990–1991							86.2	61.1	57.5	65.5	59.1		74.1	60.4	368.5	<0.05
		1996	92.9	68.0	69.4													
Swamp forest	E1	1983–1984					66.7	38.3	26.8	26.6	9.7	7.4	19.7		29.5	10.2	690.0	<0.001
		1985–1986					13.4	12.0	17.4	10.8	23.2				12.4	23.2	29.5	n.s.
	E2	1985–1986					23.9	9.1	11.1	2.0	8.7				5.9	8.7	88.0	n.s.
		1990–1991							2.5	5.7	11.8	15.7	4.2		4.0	11.6	376.5	<0.05
		1996	7.1	10.4	7.9													
Disturbed forest	E1	1983–1984					0.0	3.5	5.6	14.7	34.9	19.3	0.0		7.8	23.5	921.5	<0.01
		1985–1986					7.6	4.7	5.3	0.9	33.9				2.9	33.9	24.0	<0.05
	E2	1985–1986					0.0	11.9	20.8	19.5	30.3				18.2	30.3	64.0	n.s.
		1990–1991							11.3	33.2	30.7				21.9	28.0	466.0	n.s.
		1996	0.0	21.6	22.7							18.7	36.7					

[a]Numbers of sample days in each month and season are in Table II.

range of both groups in every study period. The proportion of swamp forest is greater in E1's home range than in that of E2.

Figure 4b shows the average proportions of vegetation types used daily, with standard deviations. These proportions are similar to the vegetation breakdown of the home range (Fig. 4a). There is a significant difference only for E1, for which the proportion of dry forest used is higher than the proportion expected from the vegetation breakdown, and the proportions of swamp and disturbed forests used are lower than expected.

When the data in Fig. 4b are pooled for each group, there is no significant difference between E1 and E2 in the proportion of dry forest used daily (Mann–Whitney U test, $n1 = 148$, $n2 = 129$, $U = 8917$, $p = 0.34$). Conversely, E1 used a greater proportion of swamp forest ($n1 = 148$, $n2 = 129$, $U = 7445.5$, $p < 0.01$), and E2 used a greater proportion of disturbed forest ($n1 = 148$, $n2 = 129$, $U = 6531$, $p < 0.001$) than the other group did. These differences seemed to reflect the different proportions of vegetation types in the northern and southern parts of the Wamba forest. These results suggest that both E1 and E2 used dry forest in similar proportions, and that they used either swamp or disturbed forest as a supplement.

The standard deviation of the proportion of dry forest used is rather small, and there is no significant difference between the deviations of different groups and periods. This means that bonobos constantly used both dry forest and the other types of forest on most of the observation days, irrespective of any differences between groups or between periods.

Table III shows the average proportion of vegetation types used in each month. Although the proportions differ from month to month, there seems to be no consistent seasonal difference in monthly use of the different vegetation types. When the data are pooled for seasons differences are apparent. Bonobos used dry forest more frequently in the rainy season and disturbed forest more frequently in the dry season, though in both cases the difference is statistically significant in only 2 of 4 comparable data sets. Conversely, there is no consistent difference in the use of swamp forest between the rainy and the dry seasons.

DISCUSSION

The application of Landsat data to surveys of vegetation types often introduces problems. First, the different combinations TM bands can yield many kinds of pictures, which suggest different vegetation maps. However, in our study three types of vegetation—dry, swamp, and disturbed forest—were easily distinguished in many combinations of TM bands, and their distributions agreed with our knowledge of the vegetation and with the vegetation map of Kano and Mulavwa (1984). Another potential problem is that the sunny and shadowed sides of slopes tend to appear as different colors, which makes it difficult to distinguish between vegetation types. However, this problem did not arise for the study area, which is situated in a very flat tropical forest.

Nevertheless, the use of Landsat data has its limitations. It was impossible to reliably distinguish between the primary forest and the old secondary forest, which comprised the dry forest category, or between the cultivated fields and the young secondary forest, which made up the disturbed forest. However, to make a more detailed vegetation map for such a wide area by actually surveying vegetation on the ground would be prohibitively time-consuming. Instead, breaking it down into 3 basic vegetation types provided valuable information for the analysis of habitat use.

The home ranges of the study groups changed noticeably from year to year, probably due to social relationships with other neighboring groups. During the group split, both E1 and E2 expanded their home ranges into formerly unused areas, then settled into new home ranges after several years. An interesting trend is that the population density of E1 was lower during a period of population increase than during periods when the population was stable or decreasing (Furuichi *et al.*, 1998).

In spite of dynamic changes in home range, the home range of both study groups in each period contained fairly stable proportions of dry, swamp, and disturbed forests. Dry forest comprised the largest proportion of the home range, and it was most frequently used in daily ranging. Many favored fruit-providing food plants, such as *Pancovia laurentii, Landolphia* spp., and *Dialium* spp., occur in dry forest. The tendency of bonobos to sleep in dry forest might also have contributed to the high proportion of its use (Kano, 1992; Idani *et al.*, 1994).

Swamp and disturbed forests were also consistently used by the study groups. Both of them provide abundant terrestrial herbaceous food (Idani *et al.*, 1994), which may be an important source of protein for bonobos, and one which is available throughout the year (Malenky and Stiles, 1991). Swamp and disturbed forests probably play an indispensable role in contributing to the bonobos' diet, even though they are used less often than dry forest.

We have shown that dry forest was used more frequently in the rainy season than in the dry season, though this tendency was not clear in both groups in study periods. Such seasonality seemed to appear because the bonobos' favorite fruits were available in the rainy season more than in the dry season. However, some favorite fruits, such as *Pancovia laurentii*, occur during the dry season (Kano and Mulavwa, 1984). Furthermore, fruiting of food trees varied substantially from year to year. These factors may explain why the difference between the rainy and dry seasons was not always clear.

Bonobos use both dry forest and swamp or disturbed forest on a daily, seasonal, and yearly basis. The combination of the 3 vegetation types may contribute to the overall stability in the availability of food resources. Hashimoto (1995) reported that a patchy distribution of secondary forest within a primary forest favored a high density of chimpanzees in the Kalinzu Forest, Uganda. The combination of different types of vegetation may also favor a high density of bonobos at Wamba (Kano, 1992; Idani *et al.*, 1994).

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REFERENCES

Elsacker, L. V. (1995). A review of terminology on aggregation patterns in bonobos (*Pan paniscus*). *Int. J. Primatol.* 16: 37-52.

Furuichi, T. (1987). Sexual swelling, receptivity, and grouping of wild pygmy chimpanzee females at Wamba, Zaire. *Primates* 28: 309-318.

Furuichi, T., Idani, G., Ihobe, H., Kuroda, S., Kitamura, K., Mori, A., Enomoto, T., Okayasu, N., Hashimoto, C., and Kano, T. (1998). Population dynamics of wild bonobos (*Pan paniscus*) at Wamba. *Int. J. Primatol.* 19: 1029-1043.

Hashimoto, C. (1995). Population census of the chimpanzees in the Kalinzu Forest, Uganda: comparison between methods with nest counts. *Primates* 36: 477-488.

Idani, G., Kuroda, S., Kano, T., and Asato, R. (1994). Flora and vegetation of Wamba forest, central Zaire with reference to bonobo (*Pan paniscus*) foods. *Tropics* 3: 309-332.

Ihobe, H (1992). Male-male relationships among wild bonobos (*Pan paniscus*) at Wamba, Republic of Zaire. *Primates* 33: 163-179.

Kano, T., and Mulavwa, M. (1984). Feeding ecology of the pygmy chimpanzees (*Pan paniscus*) of Wamba. In Susman, R. L. (ed.), *The Pygmy Chimpanzee*, Plenum Press, New York, pp. 233-274.

Kano, T. (1992). *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*, Stanford University Press, Stanford, CA.

Kitamura, K. (1983). Pygmy chimpanzee association patterns in ranging. *Primates* 24: 1-12.

Kuroda, S. (1979). Grouping of the pygmy chimpanzees. *Primates* 20: 161-183.

Malenky, R. K., and Stiles, E. W. (1991). Distribution of terrestrial herbaceous vegetation and its consumption by *Pan paniscus* in the Lomako Forest, Zaire. *Am. J. Primatol*. 23: 153-169.

Malenky, R. K., Kuroda, S., Vineberg, E. O., and Wrangham, R. W. (1994). The significance of terrestrial herbaceous foods for bonobos, chimpanzees, and gorillas. In Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., and Heltne, P. G. (eds.), *Chimpanzee Cultures*, Harvard University Press, Cambridge, MA, and London, pp. 59-75.

White, F. J. (1988). Party composition and dynamics in *Pan paniscus*. *Int. J. Primatol*. 9: 179-193.

Wrangham, R. W. (1986). Ecology and social relationships in two species of chimpanzee. In Rubenstein, D. L., and Wrangham, R. W. (eds.), *Ecological Aspects of Social Evolution*, Princeton University Press, Princeton, NJ, pp. 352-378.